

# Sublethal Effects of Resin Glycosides from the Periderm of Sweetpotato Storage Roots on *Plutella xylostella* (Lepidoptera: Plutellidae)

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**ABSTRACT** Resin glycoside material extracted from the periderm tissue of storage roots from sweetpotato, *Ipomoea batatas* (L.) Lam., was bioassayed for effects on survival, development, and fecundity of the diamondback moth, *Plutella xylostella* (L.). The resin glycoside was incorporated into an artificial diet and fed to *P. xylostella* larvae. First instars were placed individually into snap-top centrifuge vials containing artificial diet with one of six concentrations of resin glycoside material (0.00, 0.25, 0.50, 1.00, 1.50, and 2.00 mg/ml). Each replication consisted of 10 individuals per concentration, and the experiment was repeated 13 times. Vials were incubated at 25°C and a photoperiod of 14:10 (L:D) h in a growth chamber. After 6 d, surviving larvae were weighed and their sex determined, then returned to their vials. Later, surviving pupae were weighed and incubated at 25°C until moths emerged. Females were fed, mated with males from the laboratory colony, and allowed to lay eggs on aluminum foil strips. Lifetime fecundity (eggs/female) was measured. There were highly significant negative correlations between resin glycoside levels and survival, and between glycoside levels and larval weight after 6 d of feeding. For larvae that lived at least 6 d, there was no additional mortality that could be attributed to the resin glycoside material. However, there was a significant positive correlation between glycoside dosages and developmental time of larvae (measured as days until pupation). Lifetime fecundity also was negatively affected at sublethal doses. Resin glycosides may contribute to the resistance in sweetpotato breeding lines to soil insect pests.

**KEY WORDS** *Plutella xylostella*, sweetpotato, glycosides

PERIDERM TISSUE FROM the storage roots of sweetpotatoes, *Ipomoea batatas* (L.) Lam. (Convolvulaceae), produces several secondary components, including terpenoid phytoalexins, phenolic stress metabolites, proteinase inhibitors, and resin glycosides (Kays 1992, Peterson and Harrison 1992). Many of these secondary components possess biological activities (Peterson and Harrison 1992). Specifically, the glycosidic resins, which are among the most common constituents of the genus *Ipomoea* (Noda et al. 1987; 1988a, 1988b, 1988c), have antimicrobial (Bieber et al. 1986, Pereda-Miranda et al. 1993), allelopathic (Harrison and Peterson 1986, 1991, 1994; Anaya et al. 1990; Peterson and Harrison 1991a, 1991b, 1992, 1995), nematocidal (Peterson and Harrison 1992), and insecticidal qualities (Peterson and Schalk 1990, Peterson et al. 1998). These compounds also have been shown to have anticancer activity (Sarin et al. 1973, Bieber et al. 1986). The multiple defense functions of these compounds may be explained by their inhibitory effect on plasma membrane H<sup>+</sup>-ATPase activity (Calera et al. 1995).

Schalk et al. (1986) showed that a constitutive factor from the periderm of the insect-resistant sweetpotato cultivar 'Regal' (Jones et al. 1985) inhibited the growth of instars 2-3 of the banded cucumber beetle, *Diabrotica balteata* LeConte (Coleoptera: Chrysomelidae). Chromatographic techniques were used to produce an isolate from Regal periderm that accounted for much of the inhibitory activity to *D. balteata* larvae (Peterson and Schalk 1990). These isolates were the same ones that accounted for allelopathic activity, and they consist of several closely related glycosidic compounds (Peterson and Harrison 1991a, 1991b, 1995; Harrison and Peterson 1994). These materials are composed of polyester glycosides of high molecular weight (unpublished) similar to those reported to occur in other *Ipomoea* species (Noda et al. 1987, 1988b, 1994; Ono et al. 1989, 1990, 1992). Peterson et al. (1998) demonstrated that these glycosidic compounds were toxic to second instars of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), a major worldwide pest of cruciferous plants (Talekar and Shelton 1993). Peterson et al. (1998) argued that *P. xylostella* provided an excellent bioassay insect for determining the activities of secondary components from insect-resistant sweetpotato breeding lines. However, Peterson et al. (1998) bio-

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assayed only second instars and they did not report on the sublethal effects of these compounds on growth, development, and fecundity of this insect. The purpose of the research reported herein was to quantify further the toxic effects of resin glycosides from sweetpotato periderm on the survival of younger larvae (first instars), and to investigate the sublethal effects of these materials on growth, pupation, and fecundity of *P. xylostella*.

### Materials and Methods

**Preparation of Resin Glycoside Material.** Sweetpotatoes from the insect-resistant cultivar Regal (Jones et al. 1985) were grown in field plots at the Clemson University Edisto Research and Education Center, Blackville, SC, during 1996. The roots were harvested, washed, and dried. The periderm, which easily separates from the rest of the storage root (Schalk et al. 1986), was gently scraped off each root with a scalpel. To prevent interactions from stress-induced metabolites (Kays 1992), only healthy, undamaged roots were used, and any blemished areas of the roots were avoided. The periderm tissue was dried overnight at 50°C and stored frozen at -18°C.

Extraction, chromatographic separation, and preparation of the resin glycoside material for bioassays followed the procedures of Peterson et al. (1998). Briefly, the periderm tissue was extracted sequentially with hexane and methanol. Because the methanol fraction contained the antibiosis factor (Peterson et al. 1998), it was further fractionated on a Sephadex column (LH 20-100). A single fraction from this chromatographic procedure was purified using HPLC methods detailed by Peterson et al. (1998). The purified resin glycoside material was dissolved in 100% methanol and aliquots were pipetted into 30-ml solvent-resistant cups (Fill-Rite, Newark, NJ). The solvent was totally evaporated and the cups were stored at -18°C until needed for bioassays.

**Insect Rearing.** The *P. xylostella* colony originated from the Geneva 88 colony (provided by A. M. Shelton, New York State Agricultural Experiment Station, Geneva). This colony originated in 1988 and has been reared continuously since then (Shelton et al. 1991). This *P. xylostella* colony is susceptible to *Bacillus thuringiensis* variety *kurstaki* (Shelton et al. 1993a) and synthetic insecticides, including pyrethroids, carbamates, and organophosphates (Shelton et al. 1993b). The starter colony was received on 14 January 1997, and was reared continuously thereafter on a premixed, artificial diet (F9441, Bio-Serv, Frenchtown, NJ). The rearing techniques described by Shelton et al. (1991) were adapted for this study. The diamondback colony was kept in an aluminum-frame, screen rearing cage (30.5 by 30.5 by 30.5 cm) (1450B, BioQuip, Gardena, CA), which was placed in a biological incubator (model I-36VL, Percival Scientific, Boone, IA) at a photoperiod of 14:10 (L:D) h, 25°C ( $\pm 0.5^\circ\text{C}$ ), and  $\approx 50\%$  RH. Approximately 500–900 pupae were put into the cage each week. Adults were fed on a 10% sucrose solution (with two drops of yellow food col-

oring per liter) administered through a saturated cotton dental roll (1 cm diameter, 4 cm long). Females of *P. xylostella* oviposited onto aluminum foil strips hung from the top of the cage. Oviposition was stimulated by the use of collard leaf extract. To make this extract,  $\approx 65$  g of collard leaves ('Vates') and 500 ml water were boiled for 1 min. After cooling, the liquid was filtered into a jar and stored in the refrigerator (10°C). Oviposition strips consisted of pieces of aluminum foil ( $\approx 7.5$  by 12.5 cm), which were changed daily. They were dipped in the collard extract, air dried, and stored in a refrigerator (10°C) until needed. Eggs were surface-sterilized by dipping the foil strips in  $\approx 0.1\%$  sodium hypochlorite (2% Chlorox, Chlorox, Oakland, CA) for 30 s, and then rinsed in clean water for 60 s. Approximately 100 eggs were placed in each 30-ml diet cup (Fill-Rite, Newark, NJ) that contained  $\approx 15$  ml of cooled artificial diet. Larvae hatched in 2–3 d and pupated in 10–12 d at 25°C.

**Bioassays.** A preliminary bioassay experiment was conducted with the resin glycosides from sweetpotato periderm on first instars of *P. xylostella*. Essentially the same techniques were used for both the preliminary experiment and the bioassays described below. Treatment concentrations of the resin glycosides (0, 1, 2, 4, and 8 mg/ml) for the preliminary experiment were selected on the basis of the results of Peterson et al. (1998) for second-instar *P. xylostella*. Concentrations of incorporated resin glycoside material were expressed as mg of resin glycoside per ml of artificial diet. Based on the results of these preliminary experiments, the treatment concentrations for the resin glycosides for the bioassays reported in this article were set at 0.00, 0.25, 0.50, 1.00, and 2.00 mg/ml.

The resin glycoside material, which had been stored in the freezer at -18°C, was heated to room temperature and air-dried for  $\approx 1$  h. An aliquot of resin glycoside material for each treatment concentration was placed on the bottom of a 30-ml diet cup. Then 3 ml of hot artificial diet (F9441) was added to each cup, and it was immediately immersed in a water bath (model 183, Precision Scientific, Chicago, IL) at 53°C. While in the water bath, the diet-glycoside mixture was stirred for 1 min with a glass rod or plastic spatula. After stirring, the diet cup was removed from the water bath and the diet was allowed to solidify at room temperature. No sooner than 30 min after being removed from the water bath, 0.5 ml of solidified diet was packed into each 1.5-ml microcentrifuge tube (National Scientific Supply, San Rafael, CA).

To obtain a cohort of diamondback larvae, a small strip of foil with a single day's collection of diamondback eggs was placed in a diet cup with 15 ml of artificial diet 3 d before the experiment. After hatching, one neonatal larva from this cohort was placed into each microcentrifuge tube using a small camel's-hair brush (0/3), and the lid of the microcentrifuge tube was tightly closed. A small hole was made in the top of each tube with a sharp probe to prevent condensation. Care was taken to choose active larvae of a similar size for each tube. The weight of first instars ( $0.0239 \text{ g} \pm 0.0013 \text{ g}$ ) (mean  $\pm$  SE) was determined

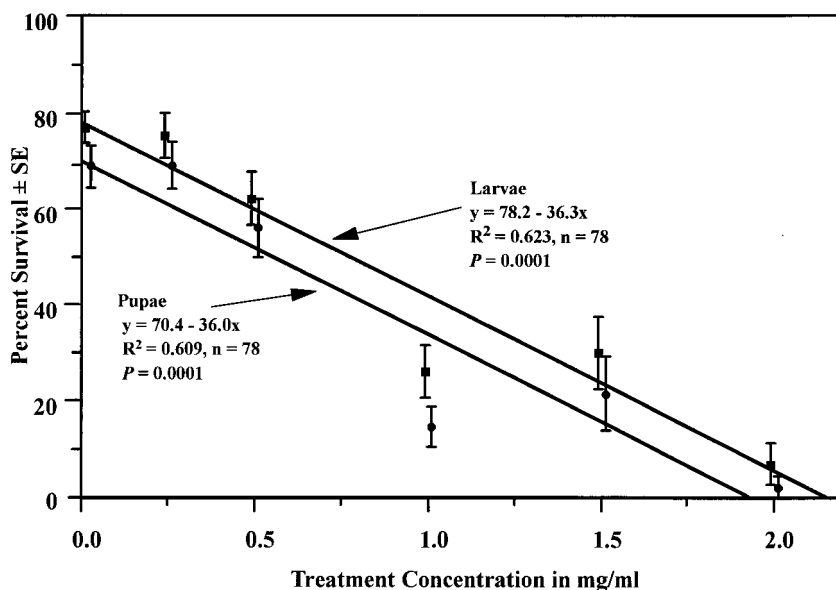


Fig. 1. Percentage survival of *P. xylostella* larvae after 6 d (top line) or until pupation (bottom line) after feeding on one of six concentrations of resin glycosides from sweetpotato periderm in an artificial diet. Vertical bars indicate mean  $\pm$  SE.

from 10 subsamples of 10 larvae each from a larval cohort on 3 April 1997. All surviving larvae were weighed (to 0.00001 g) after 6 d and then returned to their microcentrifuge tubes. Thereafter, tubes were observed daily, and sexes of larvae were determined (Liu and Tabashnik 1997). The date of pupation and pupal weight were determined for each individual. Each pupa was weighed 2 d after pupation. A wet cotton dental wick was placed in each cup in a special 1-ml holder containing a 10% sucrose solution. A newly emerged virgin male moth from the laboratory colony was put into each cup containing a female moth on the 1st d after she emerged. Male moths were left in the cups with this female for the duration of the experiment, or until he died. A collar extract-treated foil strip was added to the cups with a pair of moths. Thereafter, the date of emergence and date of death from natural causes was recorded for each adult. The foil strips were collected daily, and the number of eggs per female was recorded. The pair of diamondback moths was transferred to a new diet cup each day because a few eggs were laid in the crevices of the cup.

The experiment was repeated 13 times from 24 April to 22 August 1997. Ten microcentrifuge tubes were set up for each treatment during each repetition of the experiment. Data for 6-d larval survival, pupal survival, 6-d larval weights, pupal weights, days to pupation, longevity, and lifetime fecundity were analyzed by analysis of variance using PROC GLM and by regression analysis using PROC REG (SAS Institute 1989). Survival data also were analyzed by chi-square goodness-of-fit (SAS Institute 1989) to determine whether these data fit the Probit or Logit models (Robertson and Preisler 1992). An estimation of the effective 50% lethal concentration ( $LC_{50}$ ) of the resin

glycoside material was computed with probit analysis using POLO-PC (LeOra Software 1994).

## Results

Linear regression analyses (SAS Institute 1989) indicated a highly significant negative correlation ( $r^2 = 0.62$ ,  $n = 78$ ,  $P < 0.0001$ ) between levels of resin glycoside and survival of neonatal diamondback larvae after 6 d (Fig. 1). There was little improvement in  $r^2$  values after fitting these data to nonlinear models (logarithms, exponential, or power). Chi-square goodness-of-fit tests indicated that the 6-d survival data fit the Probit model somewhat better than the Logit model. Therefore, the  $LC_{50}$  of the resin glycoside material was determined as 0.90 (0.62 [lower 95% CI] and 1.12 [upper 95% CI]) mg/ml using the probit model (POLO-PC, LeOra Software 1994).

There also was a significant negative correlation ( $r^2 = 0.61$ ,  $n = 78$ ,  $P < 0.0001$ ) between levels of the resin glycoside and survival of larvae to pupation (Fig. 1). The slopes of the regression lines for 6-d larval survival and survival to pupation were nearly identical (Fig. 1), indicating that there was no additional larval mortality attributable to the glycoside treatments after 6 d. However, there was a significant positive correlation between glycoside dosages and developmental time of larvae (measured as days from the start of the bioassay until a pupa was found) (Fig. 2). For all treatment concentrations, it took female larvae slightly longer to reach pupation than it did male larvae. In the untreated control treatment, it took males  $8.18 \pm 0.13$  d and females  $8.56 \pm 0.15$  d to reach pupation.

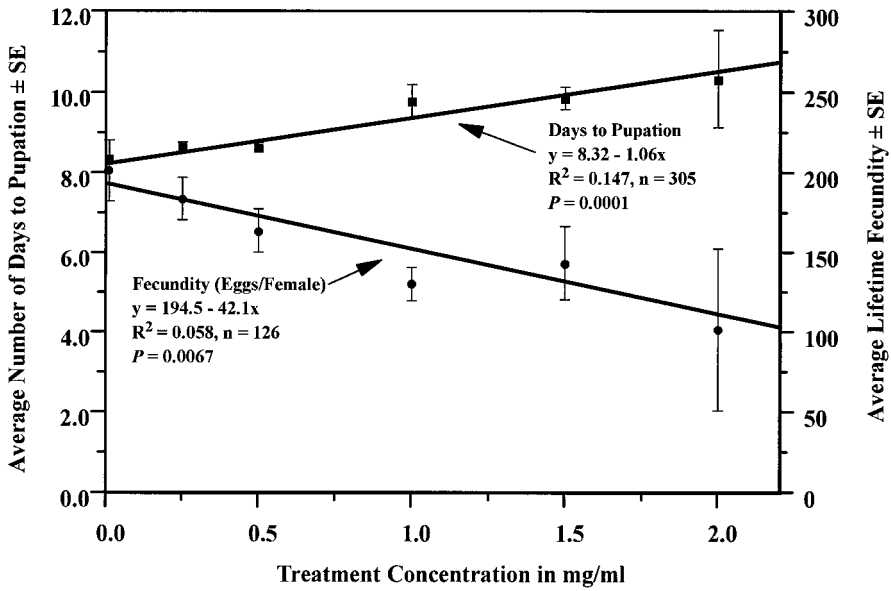


Fig. 2. Average number of days for larvae to reach pupation (top line) or lifetime fecundity (bottom line) of *P. xylostella* that were fed as larvae on one of six concentrations of resin glycosides from sweetpotato periderm in an artificial diet. Vertical bars indicate mean  $\pm$  SE.

Observations of the vials, at the time larvae were weighed, indicated that larvae appeared to feed normally on artificial diet with added glycosides. For all treatment concentrations, male larvae weighed slightly more than female larvae. After 6 d of feeding, surviving larvae in the untreated control treatment weighed  $3.62 \pm 0.30$  mg for males and  $3.56 \pm 0.32$  for females. Larval weights were negatively affected by the resin glycoside material (Fig.

3). Linear regression analysis of these data indicated a significant negative correlation ( $r^2 = 0.12$ ,  $n = 360$ ,  $P < 0.0001$ ) between larval weight and treatment concentration. This regression equation predicts a 50% reduction in weight (from the untreated control) at a resin glycoside concentration of 1.24 mg/ml.

For all treatment concentrations, female pupae weighed significantly more than male pupae. Live

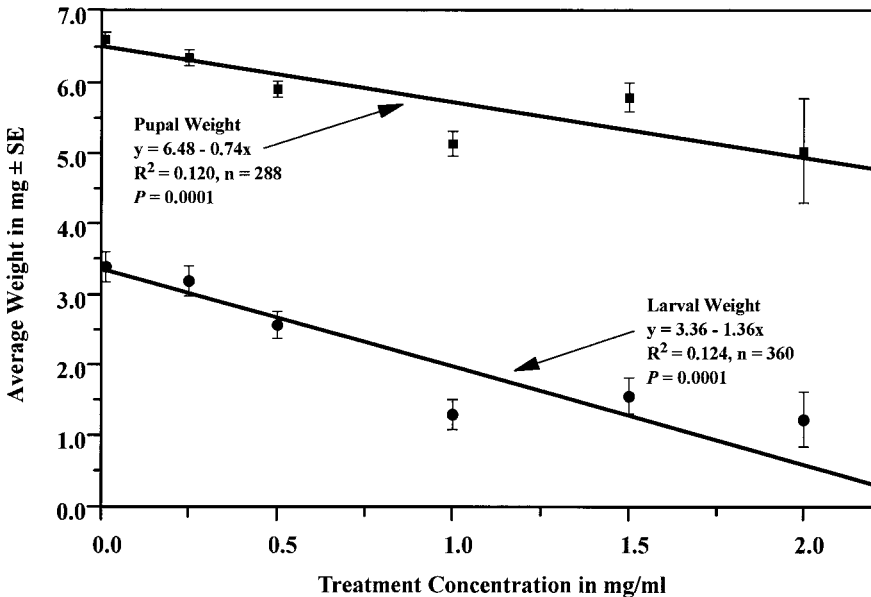


Fig. 3. Average weight of *P. xylostella* pupae (top line) or larvae after 6 d (bottom line) after feeding on one of six concentrations of resin glycosides from sweetpotato periderm in an artificial diet. Vertical bars indicate mean  $\pm$  SE.

female pupae in the untreated control weighed  $7.20 \pm 0.12$  mg, and males weighed  $6.13 \pm 0.10$  mg. Pupal weights also were negatively correlated ( $r^2 = 0.12$ ,  $n = 288$ ,  $P < 0.0001$ ) with levels of resin glycoside (Fig. 3).

Females in the untreated control produced  $201.7 \pm 18.4$  eggs. Lifetime fecundity was negatively affected ( $r^2 = 0.06$ ,  $n = 126$ ,  $P = 0.0067$ ) by resin glycosides from sweetpotato periderm at sublethal doses, although these data were somewhat more variable than the survival or weight-gain data stated above (Fig. 2).

### Discussion

It is generally assumed that insects respond to toxicants in proportion to their body size (Robertson and Preisler 1992). Thus, it is not surprising that the resin glycoside material from sweetpotato periderm was much more toxic to first instars of *P. xylostella* ( $LC_{50} = 0.9$  mg/ml) than to second instars ( $LC_{50} = 7.2$  mg/ml) as reported by Peterson et al. (1998). We believe that bioassays using first instars provide a better measure of the toxicity of these materials.

There was no additional mortality that could be attributed to the resin glycosides after the 6-d examination period, at which time most of the larvae were third instars. There was also no significant mortality attributable to the resin glycosides for pupae or adults (data not shown). However, our data show that there were sublethal effects of these materials that slow larval development, reduce pupal weights, and lower lifetime fecundity of *P. xylostella*.

Larval weights after 6 d were more severely affected (i.e., steeper slope of regression line) by resin glycosides than were pupal weights (Fig. 1). However, increased glycoside levels slowed development (Fig. 3), and all pupae were not weighed on the same day after the test began. The reduction in larval weight at 6 d is complicated by the effects of delayed development. Therefore, pupal weights probably are a better measure of the effects of resin glycosides on *P. xylostella* than larvae at a discrete point in time. Pupae represent a distinct physiological stage, whereas weights after 6 d of feeding encompasses larvae at various stages of physiological development.

The percentage survival of larvae until pupation ( $69.2 \pm 4.5\%$ ) and the weight of pupae ( $6.6 \pm 0.1$  mg) in our control treatment were similar to the values reported by Shelton et al. (1991) for diamondbacks after three generations on an artificial diet. Lifetime fecundity in our untreated control (202 eggs per female) was much higher than the fecundity ranges that have been reported in the literature (Shelton et al. 1991, Talekar and Shelton 1993). These data provide evidence that we had a nutritious artificial diet and that our diamondback colony was healthy and robust. These insects are relatively easy to raise and they perform well on artificial diet. Also, their small size makes them an ideal insect for bioassays in which natural chemical components are difficult and expensive to produce. Therefore, because of its ease of rearing and its sensitivity to resin glycosides, we believe *P. xylostella* is an ideal insect for bioassaying

sweetpotato germplasm with varying levels of resistance to other pests.

Resin glycosides from sweetpotato periderm have been shown to have several diverse biological activities (Bieber et al. 1986, Anaya et al. 1990, Pereda-Miranda et al. 1993, Harrison and Peterson 1994, Peterson and Harrison 1995, Peterson et al. 1998). The weed-suppressing potential of sweetpotato storage roots is caused almost entirely by the resin glycosides (Harrison and Peterson 1994, Peterson and Harrison 1995).

Resistance to soil insect pests varies widely among sweetpotato breeding lines (Jones et al. 1986, Schalk et al. 1991, Thompson et al. 1995, Lawrence et al. 1999). In recent studies, we (Peterson and Jackson 1998) found that sweetpotato breeding lines also vary considerably in glycoside levels. Some insect-resistant breeding lines have levels of resin glycosides approaching 2% dry weight, which is much higher than the levels that were tested in our bioassays. We believe these substances have general toxicological properties, and that they contribute to the resistance of sweetpotato breeding lines against soil insect pests. These results indicate the possibility of breeding sweetpotato with high levels of resin glycosides for the development of insect-resistant cultivars.

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